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THE SUPERNUMERARY CHROMOSOMES AND THEIR RELATION TO THE "ODD" OR "ACCESSORY" CHROMOSOME

EDMUND B. WILSON

CAMBRIDGE, MASSACHUSETTS
1909

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THE SUPERNUMERARY CHROMOSOMES AND THEIR RELATION TO THE "ODD" OR "ACCESSORY" CHROMOSOME

EDMUND B. WILSON

It has become almost a cytological dogma that the number of chromosomes in a given species is on the whole constant, the occasional exceptions to this rule being for the most part regarded as apparent rather than real, — for example, such as arise through the formation of double or multiple groups, through bivalence or plurivalence of some of the chromosomes, and the like. An examination of some seventy species of Hemiptera heteroptera, some of them represented by a large number of individuals, has in fact shown a remarkable constancy in nearly all, though a few true fluctuations, other than the merely apparent ones, have here and there been observed. A remarkable exception to this rule occurs in the genus Metapodius, where I have found in three quite distinct species (*terminalis*, *femoratus*, and *granulosus*) that the species-number is variable, though the number in any given individual is constant. Thus in *M. terminalis* individual males have been observed that show respectively in the spermatogonial divisions 22, 23, and 24 chromosomes; in *M. femoratus*, 22 and 26; and in *M. granulosus*, 23, 26, and (?) 27. A corresponding variation exists in the females of all three species, the numbers observed being in *M. terminalis* 22 and 25, in *M. femoratus*, 24 and 26, and in *M. granulosus*, 25 and 26. These variations are not correlated with the sexual characters or with any other visible structural characters. They are not casual fluctuations, since the number in each individual is constant, and the number present in the maturation-divisions is definitely correlated with that seen in the spermatogonial divisions of the same individual, as has been proved by the careful study of a very large number of division-figures, many of which have been photographed.

But a very definite order exists in this apparent chaos. When the chromosome-groups are studied in detail, more particularly in the male, it is found that the variations are due to the presence in varying number of chromosomes of a specific kind, which I propose to call the *supernumerary chromosomes*, since they may be entirely absent. These chromosomes are of small size; they always divide as univalents in the first spermatocyte-division; in the growth-period they remain in a compact nucleolus-like form; and both in the growth-period and in the second spermatocyte-division they are usually closely associated with the idiochromosomes to form a compound body.

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Study of the facts leads to the general conclusion that all the individuals possess a fundamental or type-group of 22 chromosomes, which alone are present in certain individuals. Two of these are typical "*m-chromosomes*," 2 are a pair of unequal "idiochromosomes," while 18 are ordinary chromosomes or "autosomes." In such individuals the first spermatocyte-division shows always 12 chromosomes (the idiochromosomes being, as usual, separate univalents), and the second 11. When one supernumerary is present the spermatogonia show 23 chromosomes, and the first division 13; when 2 or 4 supernumeraries are present, the spermatogonial number is 24 or 26, while the first spermatocyte-division shows 14 or 16, — *i. e.*, owing to the fact that the supernumeraries remain univalent in the first division this division shows a surplus over the type-number (12) equal to the surplus in the spermatogonia. In the second division the apparent number (as seen in polar views) is variable, owing to the fact that the supernumeraries usually couple, in a variable manner, with the idiochromosome-dyad.

Detailed study of the second division shows that the supernumerary chromosomes, when present, undergo a variable and often asymmetrical distribution to the spermatid-nuclei, — *e. g.*, when 4 supernumeraries are present each spermatid may receive 2 of them (13 chromosomes altogether), or 1 may receive 3, the other, 1 (respectively 14 and 12 chromosomes). When only 1 supernumerary is present, half the spermatids receive 11 and half 12. I believe there can be little or no doubt that the variations seen in the somatic numbers take their origin in corresponding combinations effected at the time of fertilization, these being again due to the varying numbers in the gametes.

As regards the origin of these singular conditions I believe a plausible explanation may be offered, as follows: In behavior the supernumerary chromosomes agree in every respect with the idiochromosomes; and that they are of similar if not identical nature may be inferred from their marked tendency to unite with these chromosomes during the growth-period and in the second division. In size they are usually indistinguishable from the small "idiochromosomes," though sometimes somewhat smaller. I therefore think it probable that these chromosomes are supernumerary or duplicate small idiochromosomes, the presence of which is due to a failure of the idiochromosome-dyad to divide in an earlier generation. I have in fact observed that now and then such a failure of division occurs in the second spermatocyte-division, both idiochromosomes passing to one pole. In such cases this pole receives 12 chromosomes, the other but 10; and in the former case the small idiochromosome becomes indistinguishable from a supernumerary chromosome. An egg fertilized by such a spermatozoön would possess one supernumerary; and the same would be true of half the gametes of such an individual

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(whether a male or a female). It is easy to see how from such a beginning the number might increase in subsequent generations; but there is evidently a limit to this process, since the largest number of supernumeraries I have found is five, and that in only a single individual.

This interpretation offers also a new suggestion regarding the origin of the odd or accessory chromosome. As pointed out above, a failure of division on the part of the idiochromosome-dyad leaves one pole without a small idiochromosome, and hence with only 10 chromosomes. The fertilization of an ordinary egg with 11 chromosomes would produce an individual with 21 chromosomes, including a single large idiochromosome (derived from the egg), which would be indistinguishable from an odd or accessory chromosome. I believe that this may offer a more probable solution of the problem of the origin of the odd chromosome than any hitherto advanced; and that Metapodius (which stands alone among observed Coreidæ in the possession of a pair of idiochromosomes) may represent a process of transition from the idiochromosome-type to the odd chromosome-type. This agrees perfectly with my earlier identification of the odd chromosome with the large idiochromosome, and with my suggestion that the small idiochromosome is in process of degeneration or disappearance. It further explains the apparent anòmaly that individuals that differ so considerably in the chromosome-group should show no corresponding morphological difference; for the supernumeraries, under the hypothesis, are but duplicates of the small idiochromosome, and degenerating structures at that.

If this be the correct view we should expect to find certain individuals of Metapodius with but 21 chromosomes, including an odd or accessory. I have not found such individuals in my material, but Montgomery has in fact thus described the relations in *M. terminalis;* and an examination of his preparations has satisfied me of the correctness of his account. I have previously expressed the opinion that the difference between his material and my own might be due to an error in determining the species; but I now think it not improbable that the identification was correct, and that Metapodius may actually present a case in which different individuals of the same species may possess either a pair of idiochromosomes or a single odd or accessory chromosome. If this really be the case, the explanation offered above as to the origin of the odd chromosome becomes, I think, a very probable one.

I will point out, finally, that these facts seem fatal to any theory of sex-production that operates with merely quantitative differences in the total mass of chromatin; for in these animals sex is quite independent both of the number of chromosomes and, apparently, also of the entire mass of the chromatin.

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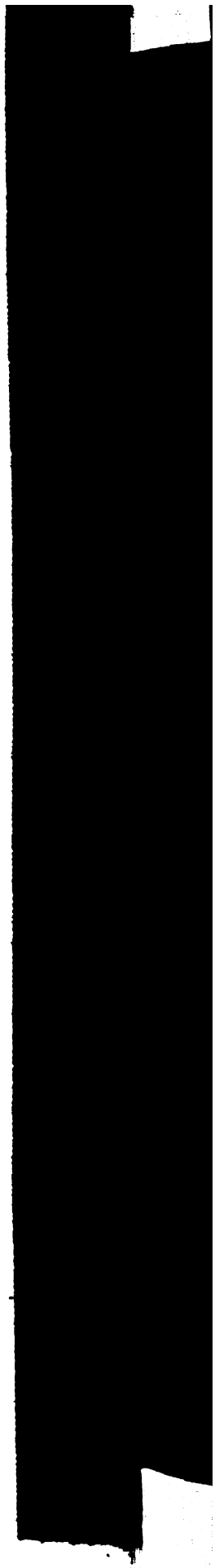

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